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Phenotypic diversity in stream salmonids: implications for conservation

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PHENOTYPIC DIVERSITY IN STREAM SALMONIDS: IMPLICATIONS FOR CONSERVATION

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ABSTRACT

Fish in general, and salmonids in particular, are known for the extent of their intraspecific phenotypic variation. Phenotypic variation allows for extension of species ranges, reduction in intraspecific competition, and adaptation to the variety of habitats to which a species is exposed. This characteristic of salmonid populations is critical for maintenance of evolutionary processes such local adaptation, differentiation, and ultimately, speciation. Phenotypic plasticity, or environmental variation, allows an individual to adjust to environmental variability and to survive in disturbed environments. And, phenotypic variation is an essential component of biodiversity, existing at the genetic and species levels and distributed in a spatial hierarchy of within streams, between streams, and between larger hydrologic units. The considerable extent of phenotypic variation in stream salmonids, including the trouts, chars, and salmon during stream-dwelling life history phases, is largely a product of the diverse habitats within their ranges and their philopatric habits. The extent and distribution of intraspecific diversity has obvious and important implications for their conservation, since conservation will require protection and restoration of habitat diversity, disturbance regimes, and genetic diversity, as well as organisms. This paper reviews 1) phenotypic variation, including its value, generating processes, and spatial distribution, 2) phenotypic variation in stream salmonids, and 3) conservation applications, including discussion of three critical components of phenotypic variation, genetic diversity, population structure, and the environmental template, and application to one stream trout subspecies, the westslope cutthroat trout.

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INTRODUCTION

Phenotypic diversity includes the intraspecific variation within and between populations in traits such as morphology and behavior, and plays a critical part in many evolutionarily and ecologically essential functions, including the ability to adapt to local conditions and disturbance regimes, population differentiation that leads to speciation, and the ability to reduce intra- and interspecific competition through niche differentiation. Fish exhibit greater intraspecific phenotypic variation than other taxa (Allendorf et al. 1997). Although each species can be characterized with regard to life history traits, considerable variation within and between populations is characteristic of most species of Pacific salmonids (Healey 1986 as cited in Gresswell et al. 1994). Recognition and consideration of this variability is critical for successful conservation of fish biodiversity at the species level (Gresswell et al. 1994). Considerable effort has been expended toward understanding genetic and life history variation in Pacific salmon, allowing for characterization and discrimination of discrete stocks (e.g. see Miller and Brannon 1981; Healey 1986 as cited in Gresswell et al. 1994; Halupka et al. unpublished manuscript). Considerably less effort has been directed toward understanding genetic and life history variation in inland trouts and chars (Gresswell et al. 1994). Yet many of the same conditions and mechanisms responsible for producing species substructuring have been documented in

stream salmonids, including homing to natal streams, genetic variation among populations, and residence in diverse and distal habitats.

Phenotypic diversity represents a critical component of biodiversity, or, "the variety of life and its processes" (USDOI and USDA 1992 as cited in Winter and Hughes 1997). Four levels in a biological hierarchy have been recognized: genetic, species, ecosystem, and landscape (e.g. Cairns and Lackey 1992), and three components at each level have been characterized: structural, compositional, and functional (Noss 1990). Alpha (species richness within a site), beta (difference in diversity between sites or populations), and gamma (diversity for a geographic area, that is a product of alpha and beta diversity; see Noss 1983, Vane-Wright et al. 1991 for discussion) diversity are terms used to describe the spatial distribution of diversity within a landscape or larger area. Phenotypic variation is biodiversity at the species and genetic levels, which is distributed in a spatial hierarchy within a species and across all of Noss' biodiversity components.

Stream habitat and faunal conditions have declined dramatically in the United States during the past 50 years, primarily as a result of land use practices, introduction of exotic species, and alterations in hydrologic regime (Allan and Flecker 1993; Richter et al. 1997). The northwestern United States is no exception to this national trend. Over 300 stocks of salmon (*Oncorhynchus* spp.), steelhead (*Oncorhynchus mykiss*), and coastal cutthroat trout *(Oncorhynchus clarki clarki*) are at risk of extinction, and four stocks have been listed as endangered under the Endangered Species Act (Allendorf et al. 1997). In the Snake River basin, coho salmon (*Oncorhynchus kisutch*) are extinct (Menke 1993). Three populations of bull trout *(Salvelinus confluentus*) have been listed under the ESA listing process. Bull trout populations have declined at 69% of sites sampled in Idaho and Montana by the U.S. Department of Agriculture Forest Service (USDA Forest Service 1993), and westslope cutthroat trout (*Oncorhynchus clarki lewisi*) was recently considered for (and denied) listing under the Endangered Species Act. As ranges and habitats decline, so do phenotypic diversity and the processes that generate it. Much of the loss in aquatic biodiversity is intraspecific, between and within populations (Behnke 1972; Echelle 1991). As aquatic systems decline, restricting species' ranges and simplifying habitats, phenotypic diversity is lost. In addition, as aquatic environments decline, the complexity of habitats at various spatial and temporal scales, and genetic diversity that makes phenotypic variation possible, are lost. Processes generating

habitat and genetic diversity are the same processes that produce phenotypic diversity, and as these processes are restricted, the potential for future phenotypic diversity is reduced as well.

Although fish exhibit higher intraspecific phenotypic diversity than most taxa, they do not express concomitant higher levels of genotypic variation. Allendorf (1988) draws two conclusions: 1) focus on only genetic diversity will fail to conserve a significant component of intraspecific fish diversity, and 2) fish are more susceptible to environmental factors than are other taxa. Phenotypic characterization of a species is critical to many conservation questions, including understanding of population structure, identification of taxonomic units to conserve, relationships between phenotypic variation and habitat complexity, scales at which phenotypic variation is expressed, and details of refuge design. Angermeier and Schlosser (1995) emphasize that the ecological and evolutionary contexts of each biodiversity component must also be considered. Conservation of not only existing biodiversity, but also the processes such as population structuring and local adaptation to diverse habitats that generate biodiversity are critical (Erwin 1991). Although phenotypic diversity such as life history and morphological differences have been used historically in conjunction with genetic information to differentiate between stocks of commercial fish species, its usefulness for addressing conservation questions is relatively unexplored. The goals of this paper are to 1) review and summarize phenotypic diversity, including description of phenotypic diversity, its values for species integrity and survival, its spatial distribution, and the processes which produce intraspecific variation, 2) summarize phenotypic diversity in stream salmonids, including salmon species during stream residence, and 3) discuss critical characteristics of phenotypic diversity and implications for conservation of stream salmonids, with specific application to the conservation of westslope cutthroat trout.

PHENOTYPIC DIVERSITY

INTRODUCTION

Phenotypic variation is the differential expression of behaviors, life history characteristics, morphology, development, or physiology, by individuals within the same species (Nikol'skiy 1969). Phenotypic variation is produced by environmental conditions (environmental variation), genetic control (genotypic variation), or a combination of the two, including interaction (GXE), such that phenotypic response of different genotypes may differ across an environmental

gradient (Berven and Gill 1983; Taylor and Bentzen 1993). Phenotypic variation may or may not be inherited; however, most traits have some degree of genetic control, and those that do not are expressions of environmental variation, or plasticity, which itself is an inherited trait (Nikol'skiy 1969). Stearns (1989) suggests that populations exhibiting diverse or unusual phenotypic patterns may also contain unusual patterns of genetic diversity.

Environmental variation is the differential response of one genotype across an environmental gradient, whereas genotypic variation is caused by differences in environmental variation between genotypes (Bradshaw 1965). Phenotypic variation under genetic control can also be caused by different genes being switched on and off. Genetic coding for traits may vary across different environments (Smith-Gill 1983). In addition to varying from trait to trait, amount of phenotypic variation may differ from species to species (Winemiller and Rose 1992); some species express significant phenotypic variation whereas some express little (Nikol'skiy 1969; Winemiller and Rose 1992). Each trait and species vary with respect to relative levels of genotypic and environmental control.

Mechanisms of evolution of environmental variation are not well understood (Schlichting 1989; Thompson 1991), but include genetic drift, local adaptation, and environmental variability (Freeman-Gallant 1996). Selection pressure is the process of environmental conditions acting on fitness, to produce genotypes with optimal response to those environmental conditions (Berven and Gill 1983). Local adaptation results when genotypes differentiate to reflect selection pressure and increase fitness of organisms across a range of environmental conditions. Developmental plasticity, heritabilities, and genetic covariances of traits among localities (geographic variation) result from differential selection pressures in each environment, and are related to developmental limitations (e.g. physiological constraints) and to the degree of compromise between traits responding to the selection pressures (Berven and Gill 1983). Genetic mechanisms of differentiation require restriction of gene flow whereas environmental variation does not, since it is not genetically based; environmental variation can therefore be produced sympatrically. Electrophoretic data would not be expected to show differences between populations for environmental variation mechanisms, whereas differences should be seen, and phenotypic markers should covary, for the other two mechanisms (Freeman-Gallant 1996). Loss of variability could occur for two reasons, genetic drift and selection (Chambers 1993). Although drift is unlikely to be effective in highly mobile species such as fish, it could be

significant where fractionation of populations could occur, such as in floodplain pools, mountain streams, and glacial lakes (Chambers 1993).

Differentiation can occur sympatrically or allopatrically (Utter 1981; Taylor and Bentzen 1993). Phenotypically distinct allopatric populations can arise in two ways: genetic differences resulting from a founder effect can initiate differentiation, or, habitat differences may produce differential selection pressures, ultimately resulting in genetic differences between stocks (Taylor and Bentzen 1993). When populations are sympatric, environmental conditions must have initiated differentiation, with genetic distinctness following as a result of selection pressures (Taylor and Bentzen 1993).

Examination of variation in phenotypic traits can contribute to understanding of the mechanisms underlying the variation and in separating environmental and genetic components (Kirpichnikov 1981). Variation in many life history traits is the result of numerous genetic and environmental factors, each contributing small amounts and at different times in an organism's life (Chambers 1993). For example, Claytor et al. (1991) found morphology and meristics of Atlantic salmon (*Salmo salar*) populations to be best explained by environmental conditions (stream gradient, distance traveled to spawning grounds); however, morphology also had a genetic component. They concluded that differences due to environmental conditions were reinforced by geographic isolation and philopatry, producing genetic differences. Schaffer and Elson (1975) found size of Atlantic salmon at sexual maturity to be a function of ocean productivity (environmental conditions) and movement patterns of the fish (genetically controlled behavior). Salmonid tendency to home to natal streams encourages genetic variation even at small scales; stocks tend to become differentiated as a result of both genetic isolation and differences in environmental conditions between streams (Schaffer and Elson 1975). In some cases, genetic and morphological patterns have been found to be similar (Echelle 1991; Schluter 1996).

Genotype plays an important role in controlling phenotypic variation. The portion of phenotypic variation that is genetic is heritability or additive genetic variation, and is the ratio of additive genetic variation to phenotypic variation (van Noordwijk 1989; Chambers 1993). Heritability is the phenotypic resemblance or similarity between parents and offspring. Genotype limits potential niche; realized niche is further restrained by biotic and abiotic environmental factors (Ryder et al. 1981). Genetic differences between populations can increase or decrease phenotypic differences between them (Ihssen et al. 1981). When acting to

decrease phenotypic differences, it is unlikely that genetic effects will overwhelm environmental effects acting to differentiate populations. Since heritability is influenced by environmental factors, care must be taken in generalizing a measured heritability to environments other than that in which it was measured (van Noordwijk 1989).

VALUE OF PHENOTYPIC VARIATION

Phenotypic variation has important value for a species in evolutionary and ecological time frames. Natural selection acts on phenotypic diversity, producing differential fitness across the range of environmental conditions to which a species is exposed (Nikol'skiy 1969; Utter 1981). Evolution is driven by differential fitness of the phenotypes. Local variation, speciation, and resilience to environmental variability are processes and functions dependent on phenotypic variation (Halupka et al., unpublished manuscript). Phenotypic variation also extends the range of a species and reduces intraspecific competition, allowing for resource partitioning (Dobzhansky 1951; Skulason and Smith 1995). Phenotypic variation allows for adjustments in response to environmental variability over the short-term while lack of genetic variation maintains stability in traits linked closely to fitness, whereas genetic variation allows for response to change over the longer-term (Kirpichnikov 1981; Stearns 1983).

Genetic diversity is an important molecular level component of phenotypic diversity. Maintaining genetic diversity preserves options for future evolution. The inherent importance of genetic diversity is its contribution to the survival of organisms, through the adaptation and optimization of their capacities to respond to a variable environment (Ryder et al. 1981). Although low heterozygosity naturally occurs and is not necessarily detrimental, loss of heterozygosity over a short period of time (several generations) can have serious implications for survival, reducing a species' capacity to respond to environmental change (Caro and Laurenson 1994; Coelho and Zalewski 1995) and correlating with lower individual fitness (Meffe and Carroll 1994).

GENERATING PROCESSES

Organisms have adapted to their environment as well as modified it. Phenotypic variation reflects historic conditions experienced by a species (Moran 1992). Therefore, maintenance of the processes and conditions present historically are important for maintaining the integrity, fitness, and evolutionary potential of the species. Mechanisms producing

phenotypic variation include genetic processes such as mutation (generating genetic diversity), genetic drift, and the founder effect, and environmental mechanisms including local adaptation, environmental variation or plasticity, and intraspecific competition (Lande 1976; Skulason and Smith 1995). Many examples can be found where phenotypic variation has been documented but understanding of causes is lacking (Holm 1988). Processes that can result in diversification within a taxon, and the full complement of existing phenotypic variation should be maintained within the ranges historically experienced or produced by the taxon. For example, Atlantic salmon from different streams that vary by gradient (and therefore velocity) and distance from ocean to spawning area vary phenotypically due to both genetic and environmental influences (Riddell et al. 1981; Riddell 1993). Differences include tail size and head mass or robustness (fish from higher gradient streams and experiencing longer spawning migrations have larger tails and more robust heads). In managing for this species, diversifying processes and phenotypic (and genetic) differences should be maintained at natural levels through the conservation of multiple stocks their natural environments (Healey and Prince 1995).

Environmental Variation

Environmental variation is a product of the diversity of environmental conditions experienced by an individual in its lifetime. Phenotypic diversity occurs at multiple spatial scales in response to environmental gradients at different scales (e.g. geology, landform, elevation at larger scales, valley form, stream channel sinuosity, gradient at medium scales, and riffle:pool, depth, embeddedness, cover availability at local scales (Healey and Prince 1995); habitat diversity must therefore be maintained at multiple scales. In addition, stream condition is largely a response to landscape and terrestrial conditions (many of the environmental variables listed above are terrestrial); therefore land management must include aquatic goals in order to maintain a diversity of natural habitats (Likens and Bormann 1974; Platts 1979; Maret et al. 1997). In order to maintain habitat diversity, historic disturbance regimes must also be maintained, since many large-scale terrestrial processes such as fire and flood are habitat maintaining. For example, low frequency, high intensity, broad scale floods are critical to channel-maintaining processes such as sediment delivery and erosional processes that maintain sediment-free substrate and large organic material within the channel (Leopold et al. 1963). In order to maintain phenotypic diversity of fishes, the range and scales of habitat diversity that produced the phenotypic response must be maintained (Healey and Prince 1995).

Fish are highly variable phenotypically, with much of that variation triggered by the environmental conditions to which individuals have been exposed. Organisms may be subjected to different selective pressures at different stages in their life cycle (Caswell 1983). In particular, organisms are inherently more sensitive to external stimuli during specific times in development, and have evolved strategies for protecting themselves from environmental heterogeneity during these sensitive times (e.g. thick egg cases, parental care; (Smith-Gill 1983). In some cases, specific environmental variables controlling phenotypic traits have been identified. However, more often, it is not well understood which environmental factors are most important for fishes (van Noordwijk 1989). All organisms are sensitive to temperature, pH, substrate concentration, and pressure, since they affect physiological processes (Stearns 1989). Environmental variables known to especially affect fish phenotype include water quality (e.g. temperature, oxygen), gradient, and food availability (Claytor et al. 1991). A wider range per environmental variable tends to produce greater differentiation in character traits (Endler 1973). Highly plastic species have evolved under conditions of environmental heterogeneity and have adapted to those conditions whereas species with little plasticity are limited to stable environments and have less capacity for adaptational change (Nikol'skiy 1969). Mean aspect and basin area explained two-thirds of the variation in spawning timing and length of spawners of Yellowstone cutthroat trout (*Oncorhynchus clarki bouvieri*; Gresswell et al. 1997). Environmental influences on salmonid development are reviewed by Thorpe (1994). Migration and movement within an individual's lifetime is a response to marginal habitats (Thorpe 1994). Timing of smoltification and maturation are dependent on prior environmental conditions related to food availability and affecting growth, and fat storage, respectively. Environmental cues at certain periods "turn on" development and later cues can halt the process. Spring temperature and stream gradient were found to explain more variation in morphology and meristics of Atlantic salmon from both sides of the Atlantic Ocean than did continent of origin (which was assumed by the authors to reflect genetic relationships; Claytor et al. (1991)). Stream gradient was most important in explaining morphometrics whereas spring temperature was more important in explaining meristic counts. Temperature modulation of development producing significant phenotypic variation is probably a universal example among ectotherms (Smith-Gill 1983).

Habitat complexity contributes to the generation of phenotypic variation. Habitat complexity has been variously defined, in terms of hydraulic variation (Pearsons et al. 1992),

depth, velocity, and substrate (Gorman and Karr 1978; Angermeier and Schlosser 1989), and structural components (McMahon and Hartman 1989). Crowl et al. (unpublished manuscript) included amount of large woody debris, bank stability, stream gradient, stream width, length of undercut bank, presence of other species, water velocity, hydraulic retention, basin area, substrate size, and amount of pool habitat, rated stream sections as having a presence or absence of habitat for each size class, and calculated habitat diversity indices (richness and Simpson's) for each stream section. According to Bisson et al. (1981 as cited in Lichatowich et al. 1995), complexity is the distribution and abundance of habitat types and their connectivity, and can be considered at multiple spatial scales. Habitat complexity is thought to influence size, structure, distribution, and stability of a population (Pearsons et al. 1992; Sedell et al. 1990) and may also increase a population's resistance to (Poff and Ward 1990; Pearsons et al. 1992) and recovery from disturbance (Connell and Sousa 1983). The buffering mechanism provided by more complex habitats may occur through the provision of refugia, providing escape and a source of colonists after disturbance events (Sedell et al. 1990). Crowl et al. (unpublished manuscript) found Colorado River cutthroat trout size structure diversity to be directly correlated with habitat complexity; however, this relationship was seen at the subbasin scale but not at smaller spatial scales. They suggest that more diverse size structures evidenced in more complex subbasins were due to the greater ability of complex habitats to provide "something for everyone," recognizing the ontogenetic niche shifts of this subspecies. Harvey (1998) found that although pools formed by woody debris tended to retain resident coastal cutthroat trout longer, overall differences in abundance and retention were slight between complex (with woody debris) and simple (without woody debris) pools. Gresswell et al. (1994) suggest that habitat complexity may affect residence time of juveniles before downstream migration, and more complex streams may contain a greater diversity of life history types than streams providing simpler habitat.

Because growth rates and organism size drive many life history characteristics, e.g. mortality schedules, age at maturity, competition and predation and therefore community structure and relationships, stream productivity can have a significant influence on species and community structure and therefore biodiversity (Werner and Gilliam 1984). Fish growth, age and size of maturation, and straying rate have been linked to stream productivity (Policansky 1983; Harvey 1998). Fish in low productivity streams will grow slowly and may be motivated to seek more productive systems, since early maturation at large size is a favored salmonid life history strategy. The evolution of migratory behavior in salmonids, including diadromy, is

thought to have occurred in response to different levels of productivity between systems and evolutionary pressure on fish to maximize growth (Gross et al. 1988). Growth rates of fish in particular are highly sensitive to changes in physical factors such as water temperature and food availability (Nicieza et al. 1994). It would therefore be expected that population and juvenile size structures would reflect stream productivity. Lower productivity streams may produce fish that spawn at an older age and larger size, and fewer small males using a sneaking strategy rather than a fighting strategy to gain reproductive opportunities (Young 1999). In general, and unlike mammals and plants, fishes apparently delay maturation under stressful conditions (Thorpe 1994). Conductivity, generally an effective surrogate for nutrient availability for streams within a basin, has been positively correlated with growth, mean size, fecundity, and size at maturity, and negatively correlated with age at maturity in lake trout (*Salvelinus namaycush*), for lake conductivities ranging from 21 to 175 μS/cm (Trippel 1993; Trippel and Beamish 1989; Trippel and Beamish 1993). McFadden and Cooper (1962) found a relationship between conductivity and brown trout (*Salmo trutta*) growth rate and standing crop of fish in Pennsylvania streams. Scarnecchia and Bergersen (1987) found a relationship between conductivity and fish production and biomass in small Colorado streams.

Finally, intraspecific competition may produce phenotypic diversity. Juvenile brook trout (*Salvelinus fontinalis*) in some streams express two feeding phenotypes, "movers" and "stayers" (Grant and Noakes 1987; McLaughlin et al. 1999). Growth of specialists for either strategy was greater than of generalists utilizing both strategies. Nielsen (1992) and Nielsen (unpublished manuscript) found juvenile coho salmon to display two feeding strategies and occupy four habitat types, resulting in differing levels of growth during their first year. She discerned four distinct phenotypes, and found that individuals remained true to their type rather than switching between phenotypes.

Genetic Variation

Genetic processes can affect phenotypic variation in various ways and at various scales. Processes which generate genetic diversity also result in the generation of phenotypic diversity. Phenotypic diversity generating processes include gene flow, isolation, and straying (Skulason and Smith 1995). Gene flow increases genetic diversity within populations but decreases differentiation between isolated or partially-isolated populations. Therefore, historic levels of gene flow must be maintained to maintain the distribution of genetic diversity and heritable

phenotypic diversity within a species (Echelle 1991). Processes such as genetic drift, or the random loss of alleles from a population, and inbreeding, act particularly strongly on small populations (Hartl and Clark 1997). Therefore, population sizes and natural population size cycles or patterns (which may include significant decreases or bottlenecks in population size) must be maintained. Combined interaction of genetic isolation, genetic diversification processes, and a variety of environmental conditions can promote genetic and phenotypic differentiation and ultimately, allopatric speciation. Extirpation of stocks must be avoided since they can represent the loss of entire genotypes and potentially phenotypes. Actions that result in the homogenization of stocks, or the disruption of genetic stock structure (distribution of genetic variation within and between stocks), such as release of hatchery stocks or mixing of stocks for supplementation purposes should be avoided since hatchery fish are typically genetically less diverse and stock uniqueness would be lost by stock mixing (Echelle 1991).

Numerous studies have documented the heritability of or genetic control over phenotypic traits in salmonids. Miller and Brannon (1981) review life history patterns in Pacific salmonids, and conclude that much of the variation in behavior and ecological traits is genetically based. Taylor (1991) reviews local adaptation in salmonids and concludes that considerable variation within species is genetically based, and that much of the variation is adaptive. Adkison (1995) concludes that one or more genetic processes, including drift, local adaptation, and founder effects, may explain the genetic component of phenotypic diversity in these stocks. Gjedrem (1976) reviews heritabilities in salmonids for the purpose of selective breeding for production, and concludes that salmonids have unusually high heritabilities for factors controlling growth rate. Age at maturity in Atlantic salmon was found to be a heritable trait (Ricker 1972; Schaffer and Elson 1975). Heavy fishing pressure on larger individuals selected for smaller (younger) spawning fish. Pink salmon (*Oncorhynchus gorbuscha*) introduced into the Great Lakes in 1956 differ significantly genetically from parent stock (Gharrett and Thomason 1987). Loss of genetic variation and genetic differences between donor and established stocks can be explained by genetic drift resulting from bottlenecks occurring immediately or throughout establishment. However, selection for physiologically tolerant phenotypes may have been necessary for this pink salmon population to become established, suggesting that adaptation and genetic changes must have occurred soon after its establishment. Other studies documenting genetic control over fish phenotypic variation include: body morphology including body weight and body shape (Gjerde 1989; Gjerde and Schaeffer 1989, rainbow trout (*Oncorhynchus mykiss* (these fish,

however, were sea farmed and may have abnormal genetic structure))); swimming behavior in response to current (Kelso et al. 1981, rainbow trout); growth, biochemical characteristics, body morphology (Riddell and Leggett 1981, Atlantic salmon); body morphology and fin size but not migratory behavior or timing (Riddell et al. 1981, Atlantic salmon); growth and maturity schedules (Wood and Foote 1996, sockeye salmon (*Oncorhynchus nerka*)); male body depth (Hendry and Quinn 1997, sockeye salmon); and body morphology, growth rate, habitat choice, spawning time and place, and age/size at maturity (Jonsson et al. 1988, Arctic char (*Salvelinus alpinus*)) .

SPATIAL DISTRIBUTION OF PHENOTYPIC DIVERSITY

Phenotypic variation may express spatial patterns. Phenotypic variation can occur at multiple spatial scales (discussed in greater detail in the Conservation Implications: Critical Issues: Gene Flow and Hierarchical Distribution Section below), ranging from behavioral variation in juvenile coho salmon (Nielsen, unpublished manuscript; Nielsen 1992) and brook trout (Grant and Noakes 1987; McLaughlin et al. 1999) within the same habitat units, to variation due to landscape-scale habitat variables (e.g. latitude (Nikol'skiy 1969; Jonsson et al. 1991)). The distribution of phenotypic diversity is largely a function of gene flow, affected by behaviors such as straying and philopatry (Taylor 1991). Species may differ considerably in the degree to which stocks vary, since degree of philopatry is also variable between species. Geographic clumping of environmental variables and therefore biological phenomena is an operating paradigm of geography. Four factors relating to stream size and position in a drainage network (area, order, link magnitude, downstream link) significantly affect species diversity (Osborne et al. 1992; Osborne and Wiley 1992). Size structure of westslope cutthroat trout was found to vary with stream size: smaller tributaries supported more juvenile trout while larger tributaries contained higher densities of larger fish (Lukens 1978). Distribution of environmental variables, and responsiveness of populations to environmental conditions, may also create a spatial hierarchy of phenotypic diversity within a species. Genetic similarity tends to increase directly with proximity (Utter 1981); however, geographic or straight-line distance can fail to correlate with genetic variation (Utter 1981; Ruckelshaus 1998). Barriers, significant events, and transport mechanisms and travel routes must be considered as well. Drainage divides, falls, introductions, hatchery releases can all affect genetic relationships of fish (Utter 1981).

PHENOTYPIC DIVERSITY IN STREAM SALMONIDS

Salmonids in general are highly variable genetically and in their life histories, within and between species (Miller and Brannon 1981; Allendorf et al. 1997). Therefore, inferences made from one species about another must be made cautiously and empirical evidence should be relied upon or gathered whenever possible.

The propensity for homing to natal streams is widely documented in salmonids; homing tends to encourage reproductive isolation and local adaptation within streams, with both environmental and genetic components (Riddell et al. 1981). Evidence from salmonids that genetic variation is spatially distributed supports the contention that salmonid populations, particularly resident populations in headwater streams, tend to be genetically isolated (Riddell et al. 1981). Salmonids tend to form local populations across various environmental gradients, partially for the reasons given above but also due to apparent plasticity in response to environmental conditions (Taylor 1991). Natural selection is most effective in species characterized by population subdivision residing in a wide range of varying environments (Wright 1931; Taylor 1991). Depauperate faunas tend to consist of habitat generalists, occupying relatively high percentages of their fundamental niches, and consequently displaying considerable phenotypic variation (Ryder et al. 1981). Both allopatric and sympatric models of divergence have been proposed for salmonids. Sympatric divergence is initiated by environmental conditions; allopatric divergence can be initiated by either genetic (e.g. drift, founder effect) or environmental factors. Both models imply a significant role for environmental conditions in divergence of salmonid species (Taylor and Bentzen 1993). Stream salmonids may therefore be phenotypically diverse within streams due to lack of interspecific competition and may have broad niche widths, and may be phenotypically diverse between streams due to genetic isolation and local adaptation.

Fish are generally responsive to stress and environmental conditions, displaying considerable plasticity (Weeks 1993). Salmonids as a group are versatile behaviorally and physiologically, with genetic variation sufficient within species to adapt to a wide range of environmental conditions (Thorpe 1994). One response to glaciation/deglaciation events has been development of rapid phenotypic response mechanisms (Echelle 1991). Variation in ability to adapt to local conditions has been demonstrated, however (Taylor 1991). Local adaptation is more likely to be seen in freshwater species and stocks exposed to strong environmental

gradients than in anadromous species (Taylor 1991). His review of local adaptation in salmonids documents variation in morphology, meristics, behavior, developmental biology, biochemical and physiological traits, life history traits, and disease resistance. Behavioral traits include migration and other adaptive movements such as ontogenetic niche shifts. Developmental rates, survival differences, and adaptations to local conditions are examples of developmental differences. Life history traits include age and size at maturity, age and size at smolt, egg size, and fecundity, timing of emergence from redds, and fry size at emergence. Kirpichnikov (1981) documents variation in length and weight among salmonids including rainbow trout and Atlantic salmon due to both environmental and genetic influences. Gjerdrem (1976) demonstrates the propensity for phenotypic and genetic change in salmonids from a cultivation standpoint, concluding that considerable variation existed between strains and families for the traits and species studied.

Life history includes reproduction, growth, mortality, and size structure. Life history traits are often co-adapted and designed by natural selection to address a particular ecological problem (Stearns 1976). Although mechanism(s) of evolution of life history traits are not thoroughly understood, Rose (1983) reviews six possible theories and concludes that antagonistic pleiotropy provides the best explanation. Antagonistic pleiotropy is the separate evolution of traits, which then interact in a competitive fashion to shape the life history pattern of each individual. Expression of each trait is moderated by pressure from other traits. Taxa can generally be placed on a two-dimensional (McLain 1991) or three-dimensional continuum of life history traits (Winemiller 1992), where the two dimensions are fecundity and juvenile survivorship and age at maturity is the third. Although organisms strive to maximize reproduction over their lifetime, an infinite number of strategies represented by locations in the continua are possible (Winemiller 1992). Location of a taxa on the continua is strongly correlated to disturbance regime and phylogenetic history (Winemiller 1992). In general, life history traits associated with fitness have little additive genetic variation (heritability; Kirpichnikov 1981). Life history traits have a genetic basis and have evolved under selective pressure; life history traits may not, however, be free to respond to selection.

Multiple Life Histories

Diverse life history patterns dampen the risk of extinction or reduced abundance in temporally variable environments (den Boer 1968). In addition, migratory forms are thought to

develop in response to low productivity environments; migration gives access to more productive systems such as oceans, larger rivers, and lakes (Gross 1988). Several salmonids have multiple life history types, including sockeye salmon (kokanee), Dolly Varden (bull trout), steelhead (rainbow trout), and cutthroat trout (e.g. coastal anadromous and resident, westslope adfluvial, fluvial, and resident). Wood and Foote (1996) found anadromous and nonanadromous sockeye salmon to differ morphologically, reproductively, and genetically. Although the two morphs reproduce in close proximity, reproductive isolation is considerable. An important factor in reproductive isolation of these morphs is body size; reproductive individuals of the two morphs do not overlap in body size and almost always choose redd sites and mates based on body size. Northcote (1970) found evidence of genetic differences between life history types in rainbow trout and reviews additional evidence for a genetic role in life history type (Northcote 1992). Genetic differences between types implies reproductive isolation and has strong conservation and evolutionary implications. Isolation means effective population sizes are smaller, and population structuring allows for local adaptation and ultimately the potential for speciation. Although many species demonstrate variation in life history traits (reviewed in Wood and Foote 1996), the relative roles of genetic and environmental factors is not clear (Schlosser and Angermeier 1995). Studies of Yellowstone cutthroat trout suggest that although life history types use the same spawning areas, they are temporally separated and little genetic interchange occurs between types (Ball and Cope 1961).

It is not clear to what extent multiple freshwater life histories are analogous to the salmon life histories of anadromy versus non-anadromy, and therefore neither is it clear whether similar evolutionary and environmental pressures drive development of multiple life histories between these species groups. Anadromy in coastal cutthroat trout suggests that the fluvial and adfluvial life histories in westslope cutthroat trout may be a freshwater version of anadromy and therefore analogous. However, significant differences exist between many anadromous migrations and freshwater movements of migratory inland trouts, including the energetic costs of long migration distances and physiological conversion to saltwater, which anadromous forms bear but which freshwater migratory forms do not. In addition, iteroparity and semelparity produce different evolutionary pressures and life history strategies (Ryder et al. 1981), and differences in community complexity and diversity of environmental gradients in habitats may produce significant divergences in life history strategy and diversity between anadromous and nonanadromous species (Taylor 1991).

Size Structure

Organism size has been recognized as an important scaling variable for comparison of various biological processes, including metabolism, growth, production rates, reproductive condition and commitments, and constraints on body size and function (Policansky 1983; Stein et al. 1987), and a considerable body of literature exists on the subject (e.g. Peters 1983; Schmidt-Neilsen 1984; Werner and Gilliam 1984). For example, van den Berghe and Gross (1984) found redd depth and female size of coho salmon to be strongly correlated, and that deeper redds are less vulnerable to flood disturbance and competition from other redd-building females. In addition, Foote (1988) found male mate choice to be dependent on male size in salmon; larger males were able to select larger females and thereby increase their fitness, since larger males tend to be more fecund and have access to better redd sites. Body size helps to explain organism distribution across habitats (Crowl et al. unpublished manuscript; Larscheid and Hubert 1992), and body size is a significant factor mediating ontogenetic niche shifts (Werner and Gilliam 1984; Stein et al. 1987). Interspecific and intraspecific competition and predation relationships can change dramatically as an organism grows and its role in a community changes with size. In understanding mechanisms of community structure and function, organisms must therefore be organized by both species and size (Werner and Gilliam 1984). Examination of community structure based on size distribution while ignoring species identities may be appropriate in some systems since many species' functional roles within a community change with size (Stein et al. 1987; Reimchen 1990). Body size can be used as an organizing principle, just as are species diversity, productivity, trophic structure, and functional processes. Body size is one of an organism's most important attributes from both ecological and evolutionary perspectives.

Environmental variation in size structure has been documented in salmonids. Crowl et al. (unpublished manuscript) found a direct relationship between Colorado River cutthroat trout size (*Oncorhynchus clarki pleuriticus*) structure diversity and habitat complexity. Different size categories of fish were associated with different habitat variables, suggesting that complex habitat supports greater population size structure diversity. Johnson et al. (1992) found size structure of brook trout in Wyoming ponds to be positively correlated with habitat variables such as depth, surface area, volume, and late-summer water temperature, and negatively correlated with extent of water-level fluctuation and a measure of recruitment potential. Larscheid and

Hubert (1992) found large brook trout to be associated with location in the watershed and channel gradient, as well as salmonid community composition. Large brook trout were associated with stream reaches lower in the watershed and of lower gradient, conditions that may result in greater productivity and therefore growth potential. Lukens (1978) found a similar relationship with westslope cutthroat trout; larger fish individuals tended to be located in larger streams and smaller fish in smaller streams. Female size in coho salmon was correlated with deeper redds, which in turn were found to be less vulnerable to flooding and competition from other redd-building female coho (van den Berghe and Gross 1984). McDonald and Hershey (1989) found size structure of a lake trout population to be influenced by angling. They sampled in 1977, prior to, and 1986, post, angler exploitation, found median size to be significantly reduced in 1986, and below the 1977 reproductive size. In addition, removal of large lake trout apparently resulted in a change in species proportions within the community; round whitefish increased and grayling decreased in abundance. Large lake trout apparently control salmonid recruitment and community structure, and therefore angling has the potential for considerable effect on the aquatic community of the study lake.

Body size has a genetic component; Smoker et al. (1994) found body size at maturity of pink salmon, particularly males, to be a heritable trait. High heritability and variation found in the study suggests that male size at maturity is not closely linked to fitness, since genetic variation in traits closely related to fitness tend to have low genetic variation. However, size variation in males has been associated with reproductive success (Noltie 1989); the relationship between male size at maturity and fitness is therefore not well understood. Size variation in females may be less due to high correlation between body size and fecundity (Smoker et al. 1994). Offspring size was shown to have a genetic component but also to be highly phenotypically plastic (Reznick 1981; Nicieza et al. 1994). Body size is strongly influenced by environmental factors such as temperature, food availability, and presence of competitors (Smoker et al. 1994). It is their hypothesis that genetic variation in body size should be less in females than in males, since genetic variation in traits related to fitness is reduced by selection, and fecundity and body size are highly correlated.

Early life history stages play a disproportionately large role in determining population recruitment (Van Winkle et al. 1993). Natural selection operates most intensively on the most vulnerable links in the metabolic and behavioral chain, which are the reproductive and early life history stages (Echelle 1991). Juveniles are susceptible to selection pressures because of their

dependence on an appropriately structured food web (Echelle 1991). Juvenile size is of critical importance for many species since larger juveniles have higher overwinter survival (Werner and Gilliam 1984). Offspring size is also associated with intraspecific competitive ability of the offspring, growth and development rates, and probability of survival through early stages of development (reviewed in Reznick 1981). These qualities affect offspring fitness. Juvenile size structure may affect juvenile timing of downstream migration, since smaller individuals have poorer migration survival (Nicieza et al. 1994). In smolting simulations, Metcalfe (1998) found that small differences in Atlantic salmon fry growth rates could affect smolt age and sex ratio, by controlling which and how many juveniles reach a critical threshold size for early smolting. Unwin et al. (1999) found incidence of parr maturation in chinook salmon (*Oncorhynchus tshawytscha*) to be linked to parr size; a minimum size threshold seemed to be operating as smaller parr never matured early.

Age at Juvenile Downstream Migration

The extent and timing of juvenile trout migration appears highly variable in inland trout (Northcote 1992). If suitable rearing habitat is available, movement may be limited to a few meters or less whereas if rearing habitat is limiting, migrations may be more extensive (Northcote 1992). Later movements of fry may be controlled by fish densities in rearing habitats and intraspecific competition. In resident populations, the majority of individuals may move very little throughout their lifetimes while a few stray out of natal streams. Nicieza et al. (1994) suggest that threshold and age at smolting in Atlantic salmon is a population-specific trait, and should be negatively correlated with productivity of natal streams. Shepard et al. (1984) found most juvenile westslope cutthroat trout to migrate from tributary streams in the upper Flathead River basin, Montana, to be age 2 (37%) or age 3 (47%), with 1% age 1 and 12% age 4. However, distribution of juveniles within these age classes varied considerably between rearing streams, with 0 to 33% age 1, 20 to 58% age 2, 33 to 60% age 3, and 0 to 25% age 4 across 8 streams sampled.

Longevity

Longevity has long been known to be associated with age at maturity: earlier age at maturity tends to shorten lifespan (Jonsson et al. 1991). Brown trout longevity has been found to correlate positively with latitude and negatively with growth rate and temperature, especially

while in freshwater (Jonsson et al. 1991). These authors conclude that longevity is primarily influenced by rate of metabolism, which is influenced by temperature. Longevity was found to vary between wild, domestic, and hybrid strains of brook trout, with wild fish living longer than domestic fish (Flick and Webster 1976). Reports of longevity in westslope cutthroat trout range from 6 (Lukens 1978) to 13 years (N. Horner, personal communication as cited in Downs and White 1997). In headwater streams, average longevity is thought to be 8 years (Downs and White 1997). Larger fish are not necessarily older since growth is spatially variable (Downs and White 1997).

Site Fidelity

Although movement has a genetic basis (Taylor 1991), the degree to which movement is genetically controlled varies and is correlated with the degree of environmental heterogeneity of a population (Thorpe 1994). Philopatry and multiple age structures are adaptive responses to temporally variable environments whereas straying and simple age structures are adaptations to spatially variable environments (Thorpe 1994). Predictable changes can be accommodated either within the range of environmental variation or by responses that are genetically programmed (Thorpe 1994). Three strategies for dispersal are described by Fahrig (1990): if disturbance is moderately frequent but highly unpredictable spatially or temporally, organisms should be highly dispersive; when disturbance is predictable in time, rhythmic or seasonal dispersal is predicted; and when disturbance is large or unpredictable, no dispersal is expected since it no longer offers an advantage to the potential disperser. At the population scale, a balance is established between numbers of individuals dispersing versus remaining, and the balance is relative to the success or survival rate of the dispersers and relative to habitat variability, such that empty habitat is successfully colonized while minimizing the number of unsuccessful dispersers (Fahrig 1990; Taylor 1991). Dispersal can increase or decrease population stability (Lomnicki 1980; Fahrig 1990); the outcome is dependent on disturbance frequency and dispersal rate. Highest dispersal occurs at intermediate disturbance rates (Fahrig 1990).

Movement behaviors such as ontogenetic niche shifts and straying are responses to inadequate habitat (Thorpe 1994). Fish generally move in response to various ecological constraints, such as the need to acquire sufficient quantities of scarce or critical resources or to escape unsuitable conditions. Movement patterns may therefore differ between streams of

differing habitat quality or resource availability. Movement often involves significant changes in environmental conditions, requiring additional phenotypic responses to flow, food, water quality, and habitat changes. Within the normal lifespan of an individual fish, habitat becomes marginal and it must seek more desirable habitat. For example, a salmonid typically moves out of its egg casing, out of the redd, out of a nursery area, into winter refuges, downstream to larger systems, and to the ocean (for anadromous species). Fish may also move from unproductive systems, since low productivity slows growth and therefore delays maturation (Policansky 1983). Northcote (1997) identifies three cyclic patterns of movement: trophic, refuge, and reproductive, all directed toward obtaining limited or patchy habitat types during critical time periods in their life history. Dispersal corridors, patch distance, disturbance distribution, and patch size affect dispersal success and population survival (Fahrig 1990). For example, increasing the numbers of patches and decreasing distance between patches increases population survival time (Fahrig 1990). Dispersal distance must acknowledge patch structure and disturbance regimes, and balance costs of dispersal with probability of success in finding suitable habitat (Venable and Brown 1988).

Dispersal represents the flow of alleles between populations, an important mechanism in maintaining genetic heterozygosity, particularly in small populations (Echelle 1991). Conversely, limited gene flow between populations can establish population genetic structuring, or β-diversity, an important component of species genetic diversity (Thorpe et al. 1981). However, straying may overestimate gene flow between salmonid populations since immigrants may have significantly lower reproductive success than residents (Riddell and Leggett 1981). Increased straying rate due to reduced or lost habitat quality or complexity may alter genetic structure, if refugees from inadequate habitat reproduce successfully. Between-stream or deme (F_{ST}) genetic variability may decline and within-stream genetic variability (V_A) may increase, at least temporarily until genetic equilibrium is reestablished (Porter 1999). Halupka et al. (unpublished manuscript) suggest that fisheries enhancement programs may reduce homing precision and increase straying rates. Actions such as these, as well as hybridization with exotics such as rainbow trout could disrupt local adaptation patterns and genetic structuring in westslope cutthroat trout and result in altered movement patterns.

Fish often differ in growth, reproduction, behavior, life history, or behavior (Ihssen et al. 1981; Chambers 1993); each individual can be characterized by a multitude of attributes characterizing that individual's phenotype and reflecting that individual's location and history

(Van Winkle et al. 1993). Following is a summary of studies documenting phenotypic variation in fishes:

Behavior

In addition to migratory behavior discussed above, Taylor (1991) reviews adaptive behaviors in salmonids, including differences in holding position in coho and Atlantic salmon and agonistic behavior in young Pacific salmon. Foraging behavior of juvenile brook trout was found to vary within still water pools (Grant et al. 1987; McLaughlin et al. 1999). Two strategies, active searching and sitting-and-waiting, were observed. Individuals tended to specialize in the use of one or the other strategies, and individuals with intermediate behaviors had lower growth potential. McLaughlin et al. (1999) suggest that behavioral variation may be an important mechanism in the evolution of phenotypic variation. Nielsen (1992) and Nielsen (unpublished manuscript) observed two foraging behaviors in juvenile coho salmon in the same pools, hierarchical territory holders and nonhierarchical floaters.

Morphology, Meristics, and Calcified Structures

Morphology, meristics, and calcified structures have been found to differ within species due to both genetic and environmental factors. Highest variation in body shape among fishes is in low current situations (Kirpichnikov). Predators and species in flowing waters, particularly those that migrate long distances, tend to show less variation in body shape. Body shape is highly related to hydrodynamic requirements of locomotion. Baumgartner (1995) identified three basic locomotory functions in fishes, cruising, accelerating, and maneuvering, and two general locomotory patterns, undulation of the body and caudal fin (cruising and accelerating), and oscillation of non-caudal fins (slow swimming and maneuvering). Body shape and fin size/shape have likely evolved to maximize performance within each fish life history strategy. Salmonids have considerable flexibility in morphology, as evidenced by significant body changes associated with spawning, and changes induced or associated with hatchery production (Fleming et al. 1984). A common morphological response is the presence of a dwarf form (Nikol'skiy 1969). In salmonids, river and/or non-migratory forms tend to be smaller than anadromous, lake, or migratory forms (Nikol'skiy 1969). Morphology and meristics often reflect environmental conditions during specific stages in development, are often irreversible, and are adaptive (Ihssen et al. 1981). Meristics have been used successfully to correlate with other

body characteristics and environmental conditions, in a variety of taxa including salmonids; however, usefulness of meristics and differences in genetic and environmental contributions between species make use of meristics a challenge unless preliminary evaluations suggest success for the species/application of interest (Ihssen et al. 1981).

Morphology includes jaw, fin, gill raker size, shape, body or head depth, stomach or gut morphology, length, and eye length. Differentiation in fishes with respect to body shape has been associated with habitat and life history characteristics (Baumgartner 1995). Taylor's (1991) review of local adaptation in salmonids documents differences in feeding morphology (e.g. mouth size and shape) of Arctic char and lake whitefish that are adaptations to local differences in available food sizes. He also documents morphological differences in pink and chum salmon (*Oncorhynchus keta*) related to flow differences in spawning streams. Riddell and Leggett (1981) and Riddell et al. (1981) found differences in body shape and fin size in Atlantic salmon that could be explained by the difficulty and distance of migration. Higher flow streams tended to produce more fusiform bodies and robust heads, and larger paired fins. These authors concluded that growth and morphology differences had a genetic basis, genetic control was minor compared to environmental influences, and the relationship between genetic and environmental influences suggested these traits were adaptive responses to spawning and rearing habitats. Fleming et al. (1994) examined morphological differences between sea-ranched, farmed, and wild coho and Atlantic salmon, and concluded that traits examined were controlled by both environmental and genetic factors. Some differences disappeared when hatchery fish were released and grown to adulthood in the wild, but some differences became greater over time between stocks longer established ranch stocks and wild or newly established ranch stocks. Captive fish tended to be more robust and to have shorter rayed fins. Claytor et al. (1991) examined meristic and morphological conditions of Atlantic salmon on both sides of the Atlantic Ocean and found stream gradient and spring temperature to explain more variation than did continent of origin. In this study, gradient was most important in explaining morphometrics and temperature was most important in explaining meristics. Hendry and Quinn (1997) found male body depth of sockeye salmon to be environmental controlled, since males spawning on shallow lake shores had shallower body depths than did males spawning on banks of flowing rivers regardless of stock origin. Body size appeared to have genetic control since it varied with stock origin; fish of differing stock origin but in streams of similar productivity were of

similar size whereas fish of the same stock origin in streams of differing productivity were of differing size.

Meristics includes fin ray, vertebra, pharyngeal teeth, lateral line scale, and gill raker counts. Because they are discrete rather than continuous data, predictive power may be reduced relative to morphological measurements (Ihssen et al. 1981). Meristic differences have been well-documented in fishes, and have been linked to environmental conditions such as temperature, oxygen, pH, and salinity (Ihssen et al 1981). Temperature during early development has been closely linked to meristic counts; cold temperatures produce larger counts (Nikol'skiy 1969). Heritability of vertebra number is high, and differences are apparently adaptive (Kirpichnikov 1981). Temperature during development and elevation (likely also a function of temperature) are factors affecting vertebra number. Number of gill rakers has been associated with salinity, and also has high heritability (Kirpichnikov 1981). Number of fin rays of most fins can vary, and variation is lower in fish in higher flow habitats. Salinity, temperature, and length of incubation have also been shown to affect fin ray number. Number of scales in the lateral line is highly variable in fishes, and is apparently controlled more by environmental factors than genetics. Determination of number of scales occurs in relatively late stages of development.

Calcified structures include otoliths, scales, bones, acellular structures, and osteology (Ihssen et al. 1981). Otolith and scale shape have been found to have stock-specific characteristics in some species (Ihssen et al. 1981). For example, scale shape placed 59-100% of whitefish into correct populations or stocks in the Great Lakes. Gorshkov (1979) found cranial differences between local populations of chum salmon. Bony structures are strongly influenced by both environmental and genetic factors; scales are more environmentally influenced than are otoliths. Chemical composition of scales has been used to discriminate between river stocks and between freshwater and anadromous stocks of salmon (Klokov and Frolenki 1970 as cited in Ihssen et al. 1981). Chemical differences between stocks represent environmental conditions, but also behavioral and physiological differences between organisms.

Reproduction

According to life history theory, individuals should employ reproductive strategies that maximize fitness, measured in terms of reproducing offspring or relative genetic contribution to the next generation (Weeks 1993). Reproductive strategy balances costs and benefits of

reproduction in one year versus potential in a later year, investment per unit, and investment in numbers of units (Schaffer 1979). Strategies are expected to change as environmental conditions change. Although reproduction is somewhat genetically controlled, much is environmentally triggered (Schaffer 1979); strategies will vary with environmental conditions and genetic history constraints, to greater or lesser extents per trait and species (Schaffer and Elson 1975; Rose 1983).

Numerous studies have documented intraspecific variation in various aspects of reproduction. Salmonids are good organisms for study with regard to reproductive variation, since they have many semi-isolated populations and express diverse reproductive strategies within and between species (Schaffer 1979). Although spawning is distributed throughout occupied ranges, migratory fish tend to use lower reaches of tributaries and resident fish tend to spawn in upper reaches (Liknes 1984). Studies of reproductive plasticity of salmonids include: fertility (Gall and Gross 1978, rainbow trout); egg diameter (Aulstad and Gjedrem 1973, Atlantic salmon); time of spawning (Kirpichnikov 1981, Atlantic salmon); investment/offspring, fecundity, time to hatch, and egg size (Hutchings and Morris 1985, various salmonids); and spawning location (Rieman and McIntire 1996, bull trout; Liknes 1984, Magee et al. 1996, westslope cutthroat trout).

Fish in variable environments may be highly plastic and genetically variable with regard to age at maturity, and early maturation at small size may be favored under these conditions (Policansky 1983). Age at maturity is heritable but expression is influenced by environmental conditions such as productivity and resulting organism body size (Wood and Foote 1996). Unwin et al. (1999) found little genetic control over maturation of chinook salmon as parr; maturation was more strongly linked to parr size. Males and females have different selection pressures, and therefore may exhibit significantly different ages and sizes of maturation. Because fecundity is strongly associated with body size, maturation in females may be driven by size as much as age, and may be more strongly influenced by stream productivity in females than in males. Multiple ages of spawning, either through iteroparity or diversity in age at maturation within a population provides important gene flow between generations and contributes to the maintenance of genetic diversity within a population (Young 1999).

Age of maturity is closely tied to growth and size in fishes. Where growth potential is limited, fish may be motivated to increase straying rates in order to increase growth and therefore maturation rate, whereas in highly productive systems, fish may have lower straying

rates and may mature early, having reached sufficient size to maximize fecundity (Policansky 1983). Increased age at sexual maturity should be expected in poorer growth conditions, since growth and size are critical factors in maximizing reproductive output (Nicieza et al. 1994). However, In harsher environments, where larger size of offspring increases survival, greater parental investment in offspring may be expected (Weeks 1993). When lifespan is decreased, earlier reproduction will be favored (Weeks 1993). Resident fish may mature at a smaller size and earlier age, and may spawn earlier in the season (Northcote 1992). When life history characteristics do not match environmental conditions, or response of a species is expected but not seen, several possibilities can explain the mismatch. Environmental heterogeneity may be such that parents and offspring do not experience the same conditions, such that offspring success is not modified by parental adjustment in strategy or parental adjustment is not made because difference in parent/ offspring condition is not perceived by the parents. Or, parents may lack necessary mechanisms to adjust strategies in response to environmental conditions (Weeks 1993). Schaffer and Elson (1975) found age at maturity to vary in Atlantic salmon in response to migration distance and ocean growth rate.

Winemiller and Rose (1992) examined patterns of reproduction for 216 families of North American fishes, and found significant correlations with phylogeny, migration behavior, and other life history characteristics. Freshwater salmonids tended to be characterized by larger size, larger clutches, fewer spawning bouts, and greater investment in parental care per offspring; however, considerable variation was demonstrated between species. Anadromous salmonids had similar tendencies but were less extreme in body size, clutch size, and spawning characteristics relative to non-salmonids. Precocious or "sneaker" males of small size have been documented for a variety of salmonid species, particularly in streams with greater habitat complexity (Gross 1985; Gross 1991; Halupka unpublished manuscript). Young (1999) documented variation in age at maturity in male coho salmon between two neighboring basins on the Oregon coast. Proportion of males spawning as "jacks" was positively correlated to spawner density. Jack proportion was also negatively correlated with spawning stream conditions, including gradient, elevation, and smolt and adult migration distance. Precocity is controlled both genetically and environmentally in coho salmon. Wood and Foote (1996) examined genetic, morphological and reproductive characteristics of anadromous and nonanadromous sockeye salmon, and found that although the two morphs differed in many genetic and life history traits, they did not differ in age at maturity. They did, however, find age

at maturity to be closely related to size within both groups. Unwin et al. (1999) found a small but significant proportion (2.1-6.8%) of male chinook salmon in two New Zealand hatcheries matured as parr and that these parr were capable of surviving and reproducing again under hatchery conditions, and suggest that a continuum may exist between iteroparous and semelparous life history strategies in salmonids.

Genetic Diversity

Quantity and distribution of genetic diversity within species is highly variable in salmonids (Ryman 1983). Miller and Brannon (1981) suggest that genetic programming in salmonids would be expected to vary between species and even within species between ontogenetic phases and in different habitats, based on variation in selection pressure and significance to completion of a complex life cycle. Salmonid tendency to home to natal streams encourages genetic variation at local spatial scales (Riddell et al. 1981). Species occupying habitats that are easily fragmented, such that gene flow is limited, and such as mountain streams, glacial lakes, and floodplain pools, are more likely to suffer from reduced genetic heterozygosity than are other populations (Chambers 1993). Rainbow trout contains an extremely high total quantity of genetic diversity; brown trout and sockeye salmon represent low (65%) and high (95%) extremes of percent genetic diversity contained within populations, respectively (Ryman 1983).

CONSERVATION IMPLICATIONS FOR STREAM SALMONIDS

Conservation efforts for stream salmonids must consider critical conservation issues and goals, and specific phenotypic characteristics of the species of interest. This section will 1) identify critical components that must be addressed for species conservation, 2) discuss conservation issues relevant to stream salmonids, and 3) apply these considerations to the conservation of westslope cutthroat trout. Conservation must be considered in short-, mid-, and long-term time frames, as well as across spatial scales of relevance to the species being conserved. Restoration or maintenance of critical processes must be considered, as well as ways to limit or control processes detrimental to maintenance of phenotypic diversity and diversifying processes. In addition, components of phenotypic diversity, including structure, composition, and process, must be considered. In particular, maintenance of diversifying

processes will allow for the potential for phenotypic diversity in the long-term, even if structural or compositional components have been lost (Angermeier and Schlosser 1995). Critical components of a species' phenotypic diversity include maintaining genetic diversity within the species, which allows for evolution and local adaptation, maintaining the habitat template of a species that promotes local adaptation and plasticity, and maintaining the population structure of a species, including rates of gene flow and distribution of genetic, phenotypic, and habitat diversity across spatial and temporal scales (Riddell 1993; Healey and Prince 1995). Management and conservation challenges include elucidation of the most meaningful taxonomic units for conservation, differences and similarities between levels of biodiversity and therefore the effectiveness of conservation strategies aimed at multiple levels, habitat protection and reserve design as well as management of unprotected populations, maintenance of the evolutionary potential and resilience of populations, species, and communities, and questions associated with the reintroduction of species into extirpated ranges.

CRITICAL COMPONENTS

Genetic Diversity and Diversifying Processes

Maintenance of the structure of genetic diversity within a species is critical to its sustainability across its range (Taylor and Haas 1996). A species may be genetically diverse for some traits and homogenous for others. If a metric trait remains under constant selective pressure, selection should eventually erode additive genetic variation for the trait (Stearns 1983). Heritability (additive genetic variation) can thus be used to infer relative selection pressure on different traits. Traits closely related to fitness are expected to have little additive genetic variation (canalization), since strong directional selection pressure in the past would have selected for the optimum (Lewontin 1974; Kirpichnikov 1981; Berven and Gill 1983; Falconer 1989). Conversely, plasticity in traits indirectly linked to fitness may allow a species to thrive in a wide range of environmental conditions and in highly variable environments, spatially and temporally (Thorpe 1994). Plasticity in some traits provides important buffering of an organism from environmental variability, without requiring compromise on traits canalized to maximize fitness. The relationship between phenotype and genotype can therefore reveal information regarding the evolutionary history of a population. Examination of the relationship between genetic and phenotypic diversity, and distribution of genetic diversity among traits, can

provide important clues to the environmental conditions to which the species is exposed, and its strategies for maximizing fitness within their constraints.

Genetic diversity allows a species to respond to environmental changes over evolutionary time frames (Meffe 1986). Loss of genetic information represents a loss of that potential for response. Some fish stocks are more vulnerable to loss of genetic diversity than are others. Extent of stock structure in populations and life history features are the primary determinants of vulnerability (Thorpe et al. 1981); salmonid species differ considerably in their level and distribution of genetic diversity within species (Utter et al. 1980). Stock structure influences processes such as genetic drift, gene flow, and selection. Species such as Pacific and Atlantic salmon, which are subdivided into partially to almost entirely isolated stocks, are vulnerable to both reduction of overall genetic diversity through loss of stocks and loss through directional changes in genetic composition (Thorpe et al. 1981). Although many salmonid species occur naturally as small, semi-isolated populations, and population structure and isolation allow for phenotypic differentiation between populations, decline in population size below historic lows, or for longer than natural periods, threatens to reduce genetic diversity in these declining populations. Minimum viable population (MVP) size concepts have not been applied to stream salmonids, but MVP sizes are likely to differ between species (Riddell 1993). Genetic processes such as drift and inbreeding, which result in the loss of genetic diversity, act more strongly on small populations, and may be the cause of accelerated loss of genetic information that can not be countered by mutation and genetic exchange between populations (Meffe 1986; Hartl and Clark 1997). Maintenance of effective population sizes at natural levels is critical to avoid increasing the loss of genetic information through these processes (Utter et al. 1980). Mixing of hatchery and wild fish may dilute natural genotypes and selective harvest may alter genotype and phenotype frequencies within a species, reducing genetic diversity and altering population structure within the species (Reisenbichler 1997).

Environmental Template

Phenotypic response is influenced by spatial and temporal variation. Environmental variables at multiple scales provide a template to which a species' genotypic and phenotypic variation respond (Healey and Prince 1995). Conservation of the full range of habitats for the species is critical to maintenance and development of that species' full complement of genetic and phenotypic variation (Healey and Prince 1995). Salmonid species typically consist of

isolated or partially isolated populations that are differentiated genetically and phenotypically, with each populations adapted to the environmental conditions of its particular stream (Taylor 1991).

Environmental heterogeneity within an individual's lifetime should favor development of environmental variation (environmental plasticity), whereas environmental heterogeneity across generations should favor genetic plasticity for life history and energy investment strategies (Giesel 1976; Weeks 1993). Intensity and frequency of environmental change provide important selection pressures (Schlichting 1989). In order for a phenotype to be functional, often several or multiple traits must be integrated, yet changes in the environment alter relationships between traits and the optimum for all environmental conditions can not be attained (Schlichting 1989). Organisms may not be able to respond immediately or to frequent changes in their environment and often pressures in opposite directions for different traits must be balanced. Organisms ultimately respond optimally to the set(s) of conditions experienced most commonly (Via 1988). Relationships between plasticities of various traits represent real constraints on adaptation to heterogeneous environments. Organisms in a stable environment may achieve complete integration of phenotypic traits, to produce highly adaptive phenotypes for their narrow range of environmental conditions, whereas intermediate levels of integration and phenotypic plasticity (a generalist strategy) may be the most successful for organisms in moderately to highly variable environments. Complex stable environments allow for the development of multiple specialist phenotypes whereas highly variable environments may limit differentiation to a few generalist strategies. For example, complex environments have been associated with more diverse size structure in Colorado River cutthroat (Crowl et al., unpublished manuscript) and Gresswell et al. (1994) suggest complex habitats may contain a greater diversity of life history types than streams providing simpler habitat. Precocious males of small size have been documented for a variety of salmonid species, particularly in streams with greater habitat complexity (Gross 1985; Gross 1991; Halupka unpublished manuscript). Stability and complexity of environments on multiple temporal and spatial scales interact to produce an environmental template to which a species must respond.

Phenotypic variation (plasticity) tends to be spatially clumped, associated with certain environmental characteristics or as a result of phylogeny. For example, greater variation is seen within a species at northern temperate latitudes, where environmental gradients are wide, compared to tropical and extreme latitudes (Nikol'skiy 1969). Within fishes, salmonids and

some cyprinids tend to be more phenotypically diverse than other groups (Nikol'skiy 1969). Phenotypic diversity is also seen, for example, in the upper Great Lakes, where dominant taxa have diversified to exploit scarce biotic resources in large, austere, spatially diverse oligotrophic systems (Ryder et al. 1981). Phenotypic diversity occurs in generally diverse habitats separated by ecological barriers or in response to intense predation (Dobzhansky 1951). In populations with phenotypic plasticity, spatial variation produces individual differences, based on differential response to environmental conditions. Population structure based on age does not adequately describe populations, since individuals within an age group vary (Schaffer and Elson 1975; Caswell 1983; Policansky 1983). Fine-grained spatial variation produces individual differences within a population, whereas coarse-grained variation produces interpopulational differences (Caswell 1983).

Differentiation is associated with temporally variable environments, for example in "empty" niches (post-disturbance locations, e.g. post-glaciation mountain lakes; Dobzhansky 1951; Stearns 1981; de Jong 1990; Taylor and Bentzen 1993; Skulason and Smith 1995). Perturbations can occur over a variety of time scales, from those producing immediate behavioral or physiological response, through lengthier scales of response to an evolutionary scale (Ryder et al. 1981). The latitude of phenotypic response is set by genetic limits, but many phenotypic traits are plastic and the range of potential responses is broad. When temporal variation is fine-scaled, demographic differences are masked and age-based population structuring adequately describes the population (individuals within an age group are identical; Caswell 1983). However, coarser-grained temporal variation leads to variation in age:size relationships such that differentiation within an age group is seen. Organisms living in frequently disturbed environments should express relatively high rates of dispersal, in order to escape marginal habitats, take advantage of newly available habitats, and spread risk and increase fitness by distributing offspring such that some reach appropriate habitat (den Boer 1981).

Population Structure and the Hierarchical Distribution of Diversity

Phenotypic and genetic variation can be seen at various spatial and temporal scales (Taylor 1991) and occurrence of ecological processes over the landscape is scale dependent (Morris 1987; O'Neill et al. 1988; Carlile et al. 1989; Lewis et al. 1996; Rabeni and Sowa 1996; Cooper et al. 1998). Activities such as release of hatchery fish, transplantation of wild fish, and selective harvest may disrupt genetic and phenotypic population structures, reducing genetic

diversity and encouraging outbreeding depression and loss of locally adaptive phenotypic variation (Reisenbichler 1997). Mason and Brandt (1996) found models of fish growth rate potential to vary across both spatial and temporal scales. The scales at which adaptive divergence occurs may be related to local hydrology and physiographic barriers to gene flow, and may be trait-specific (Taylor 1991). Relative importance of environmental and genetic factors controlling phenotypic response may vary with temporal and spatial scale of variability in the environment, and the interactions between them (Riddell and Leggett 1981). The relative importance of competition, predation, and abiotic factors may change with scale and species identity (Menge and Olson 1990). Response of organisms to disturbance is dependent on the relationship between the scale of disturbance and the range of scales on which an organism is able to respond phenotypically (Thorpe 1994).

Processes within species occur at different spatial scales, and conservation of fishes depends on consideration of the multiple scales at which they operate (Addicott 1987; May 1994). Scales at which organisms operate can be dependent on resource distribution; sparse resources and multiple critical resources require an organisms to operate on larger spatial scales, whereas substitutable resources ease scale requirements (O'Neill et al. 1988). Pacific salmon phenotype and genotype vary on multiple spatial scales; the population scale was most important to genetic variation whereas the ecosystem and landscape scales were most important to phenotypic variation (Healey and Prince 1995). Proportion of jack spawners in coho salmon differed in relation to local stream habitat variables including gradient, distance from the ocean, and elevation, but not in relation to the larger scale variable of basin identity (Young 1999). Phenotypic variation can be seen at very localized spatial scales; increasing geographic distance will promote adaptive divergence due to both the reduced potential for gene flow and increasing differences in environmental conditions (Taylor 1991).

Ecological processes operate at various temporal scales, and phenotypic response is expected to reflect those scales. Effects of perturbation can be expressed over a variety of time scales, from immediate response through to an evolutionary scale (Taylor 1991). No single time scale can be applied to biological systems; response times should be expressed as numbers of generations when comparisons are to be made (Ryder et al. 1981). Rate of adaptation to environmental change is dependent on factors such as population size, relative intensities of local selection within populations, gene flow among populations, and extent of environmental and genetic plasticity present within the population (Taylor 1991). Considerable differentiation

has occurred in North America in the past 15,000 years, since most has occurred post-glaciation (Taylor 1991). Gharrett and Thomason (1987) suggest that adaptive differentiation has occurred in pink salmon since their introduction into the Great Lakes in 1956, and Lannan (1980) has observed change in developmental rate of hatchery stocks of chum salmon in only 6 years. Morrissy (1973) documented naturalization of rainbow trout introduced into Australia in the past 100 years.

Species consist of a spatial hierarchy of genetic structure (Riddell 1993; Meffe and Carroll 1994). Genetic diversity can be partitioned into within-population and among-population components, and biologically significant breaks in diversity, and therefore scales at which significant diversity is located, can be identified (Meffe and Carroll 1994). The genetic hierarchy is a product of biologically meaningful geographic hierarchies in the distribution of species. Riverine species represent a clear example of both geographic and genetic hierarchies, since rivers form a geographic structure with a natural hierarchy (Meffe and Carroll 1994). Genetic conservation must be considered on three time scales: days to decades for maintenance of viable populations in the short-term (extinction avoidance), decades to thousands of years to maintain the ability to continue adaptive evolutionary change, and thousands to hundreds of thousands of years, to maintain the capacity for continued speciation (Meffe and Carroll 1994). Failure to succeed at the shorter time scales will preclude success at longer time scales. Genetic change on longer time scales may reflect modifications expressed on shorter time scales. Local populations of nonmigratory freshwater salmonids carry a relatively small proportion of total species genetic diversity; much genetic variation is contained between local populations (Allendorf and Phelps 1980; Gyllensten 1985; Riddell 1993). Distribution of genetic diversity within taxa is primarily a result of patterns of gene flow (Echelle 1991; Meffe and Carroll 1994). Gene flow may be the only significant contributor of new alleles into a small population, since mutation is too slow and genetic drift will overcome selection favoring allele diversity (Echelle 1991). Genetic population structure defines the rate and spatial scale at which populations can evolve in response to environmental variability. Allendorf and Utter (1979) suggest a correlation between allelic heterozygosity and heritability of morphological characteristics and expression of phenotypic traits.

MAINTENANCE OF EVOLUTIONARY PROCESSES

At one time, ecologists believed environmental variation damped evolution (Stearns 1980) and uncoupled the phenotype from the genotype, slowing the rate of trait evolution and adaptation (Wright 1931). Rapid evolution of environmental variation and its evolutionary importance is now accepted (Caswell 1983; Stearns 1983; Thompson 1991). Even Darwin identified plasticity as a mechanism, though minor, in evolution (Nikol'skiy 1969). In addition to inheritance of specific phenotypic traits, an organism inherits the trait of plasticity, or capacity for change. This property allows organisms to respond and adapt to environmental changes through modification of structure, behavior, and other life history characteristics (Nikol'skiy 1969; Utter 1981). This potential for variation feeds evolutionary processes. Selection acts on individuals differentially, based on their unique characteristics, and differential reproduction results in changes in allele frequencies, a first step toward speciation, and ultimately, evolution (Skulason and Smith 1995). Local variation, speciation, and resilience to environmental variability are processes and functions dependent on phenotypic variation (Halupka et al. unpublished manuscript).

Phenotypic variation extends the ecological range of a species, exposing species to new selection pressures and creating new opportunities for genotypic and phenotypic response (Dobzhansky 1951). Phenotypic divergence is one response by a species to intraspecific competition and allows for resource partitioning, which can lead to sympatric divergence and speciation (Skulason and Smith 1995). At the same time, genetic variation constrains and directs the pathways of evolution (Maynard-Smith et al. 1985). Understanding patterns and processes of variation, both genotypic and environmental, is critical to the understanding of evolutionary phenomena (Stearns 1989). Loss of diversity can result in reduced evolutionary flexibility and decline in fitness (Meffe and Carroll 1994). Causes, consequences, and evolutionary potential of phenotypic plasticity are important questions in the ecology and conservation of organisms in variable environments (Schlichting 1989). With the reality that conservation efforts are limited and choices must be made, conservation of genetic diversity and evolutionary processes should be priorities (Echelle 1991; Templeton 1994).

Phenotypic variation is essential to the maintenance of fitness at individual and population scales. Fitness, or the contribution of an individual in a breeding population to subsequent generations (Larkin 1970), is a property of an individual and is also a property of a population (Kapuscinski and Lannan 1986). Maintenance of fitness should ensure an adequate

degree of genetic diversity to enable a species to perpetuate in the face of environmental change, natural mortality, and stochastic events (Kapuscinski and Lannan 1986). Environmental variation in some traits may allow adjustment to variable environments while maintaining stability in traits closely linked to survival and fitness (Stearns 1983). For a species, the variation in fitness is determined by life history and reproductive strategies, and reflects genetic variation necessary for adaptation through the range of environments encountered by the population (Kapuscinski and Lannan 1986). Traits associated with fitness tend to have low genetic variation or heritability (Kirpichnikov 1981).

Local adaptation is the process by which natural selection increases the frequency of traits contributing to survival and increasing fitness of individuals expressing them (Taylor 1991). Adaptation through response to environmental conditions, even prior to genetic change, may be a common mechanism of evolutionary change in north temperate fish faunas (Taylor and Bentzen 1993), and may explain much of the genetic variation observed between fish populations, controlling differences in morphology, meristics, behavior, development, physiology, biochemistry, and life history traits (Taylor 1991). Local adaptation is an important factor contributing to the genetic diversity within salmonid species, and therefore their stability and persistence (Taylor 1991). The unsuccessful transplantation of fish stocks provides many examples of the significance of local adaptation and the role of environmental characteristics in shaping fish population phenotype and success in a given environment (Taylor 1991).

UNDERSTANDING AND MAINTENANCE OF POPULATION STRUCTURE

Fish communities are being widely affected by anthropogenic effects such that genetic and phenotypic diversity are being lost. Focusing conservation efforts on species or subspecies will fail to conserve diversity within the taxa (Behnke 1972). Fish species are subdivided into more or less discrete populations and subpopulations (Berst and Simon 1981), characterized by their distribution, genotype, and phenotype and reflecting some level of reproductive isolation (Taylor 1991). Elucidation of fish population structure through examination of genetic and phenotypic variation within and between populations can help to define meaningful units for conservation (Lomnicki 1980; see Units of Conservation section below for further discussion). Genetic population structure has important implications for the ability of species to respond to environmental conditions and variability (Caro and Laurenson 1994). Genetic diversity and structuring allows for local adaptation and continued speciation (Ryder et al. 1981; Meffe 1986),

and from a knowledge of population structuring, important demographic information such as effective population size and gene flow can be estimated (Loeschke et al. 1994 in Porter 1999).

MAINTENANCE OF RESILIENCE IN HETEROGENEOUS ENVIRONMENTS

Local adaptation is an important contributing factor to genetic diversity and therefore stability and persistence of a population (Taylor 1991). Communities that are most resistant to disturbance and therefore are the most resilient are those most frequently and predictably disturbed, such that adaptive responses exist within the community (Reice et al. 1990). However, anthropogenic stresses such as harvest, habitat degradation, and pollution may alter adaptive mechanisms and reduce genetic, phenotypic, and species diversity, and therefore resilience. Resilience may be reduced since variability of biological matter is essential in allowing organisms to cope with environmental variability (Kapuscinski and Lannan 1986; Pimm and Hyman 1987).

CONSERVATION STRATEGIES AND SURROGATES

Genetic variation is essential for maintaining evolutionary processes and species fitness. Patterns of phenotypic variation within species may be reasonable surrogates for genetic variation. Cheverud (1988) found genetic and environmental control over phenotypic variation acted on growth and development in a similar manner. Although the direction of phenotypic variation may not be identical to that of genetic variation, they were similar in a variety of taxonomic groups, including birds, fish, and rodents (Schluter 1996). Although much remains to be learned regarding the relationship between genetic and phenotypic diversity, phenotypic variation could facilitate conservation of genetic diversity and its processes since it is easier and less expensive to measure (Schluter 1996).

Conservation efforts can not afford to focus on single species. Requirements of conservation efforts limited to a focus on species and populations will exceed available resources and societal tolerance (Franklin 1993; Schlosser and Angermeier 1995), are too slow to match the rapidity with which many species are declining, and are too inefficient (Franklin 1993; Angermeier and Schlosser 1995). Methods focused on single-species approaches are proving ineffective (see Orians 1993). In addition, many species have not yet been identified and their status (and potential peril) are unknown (Franklin 1993; Schlosser and Angermeier 1995). Finally, species-level focus runs the risk of pitting species' needs against each other;

conservation strategies above the species level will by necessity balance needs of multiple species (Moyle and Yoshiyama 1994). Assemblage-level focus must be a mainstay of efforts to conserve aquatic biota. Franklin (1993) emphasizes the need for ecosystem and landscape perspectives, citing many of the limitations of a species approach listed above. However, it may be premature to shift to a larger scale community focus since community processes are complex and insufficiently understood and necessary tools may be lacking (Rieman personal communication). Lessons from single species approaches may be applicable to community perspectives, serving as stepping stones from familiar to new territory (Rieman personal communication). Examination of individual species may also provide direct information regarding the nature of a community's response to environmental shifts in condition or disturbance regime. If species have evolved together over time, components of a community are likely to have become coordinated (Ryder et al. 1981). Competition for niche space will ultimately result in a steady state or "harmonic community" (Ryder et al. 1981). This does not mean that natural systems are static, but that they fluctuate in relative abundances with environmental variability. Species that have evolved together in a community make adjustments in response to fluctuations in environmental conditions. Changes in an integrated community in response to changes in environmental conditions and variability may be seen in individual components of that community (Ryder et al. 1981).

UNITS OF CONSERVATION

Conservation efforts will be ineffective if targeted at taxonomic units that are not meaningful to species integrity and survival or that fail to include significant components of species diversity, or if spatial distribution of phenotypic variation and relationships to landscape variables are not considered. Every unique component of a species can not realistically be conserved. Genetic variation has been detected between very localized populations, and as genetic differences become detectable at finer and finer scales, their individual management becomes increasingly impractical (Riddell et al. 1981). Working below the level of populations in most instances becomes prohibitively expensive and time consuming. However, to conserve only higher taxonomic levels overlooks important dynamics and attributes of individual populations and risks the loss of local ecological function and genetic diversity (Meffe and Carroll 1994). Criteria for identifying conservation units include long term geographic isolation, geographic distance, distinct life histories or behaviors, and significant genetic difference. The

population is the ecologically and evolutionarily functional unit, since it is the unit over which local adaptation and genetic change occurs (Riddell et al. 1981; Meffe and Carroll 1994). Defining management units as populations provides a compromise between managing each genetically differentiated unit and the availability of management effort while minimizing loss of genetic resources (Riddell et al. 1981). The best strategy for preserving management and evolutionary options is to maintain as many populations as possible while retaining natural patterns of genetic diversity within and between populations (Echelle 1991).

Because the population is the most appropriate level for conservation, better understanding of its definition and functions is essential (Meffe and Carroll 1994). Management needs and priorities should be based on knowledge of geographic patterns of genetic or phenotypic differentiation (Echelle 1991). Genetic information regarding discreteness of stocks is not sufficient on its own to define units for conservation (Riddell et al. 1981); stocks may be genetically indistinguishable but differently adapted to their respective environments (Utter 1981). Although allele frequency information may be useful in identifying discrete stocks in management units, it is of limited utility in making decisions regarding management, since one must assume that gene frequencies are correlated with fitness (Kapuscinski and Lannan 1986). The specific loci assayed biochemically will not be responsible for phenotypic differences, and may be irrelevant to the characterization and survival of a population (Echelle 1991). However, focus on phenotypic diversity may result in the failure to seek and therefore detect genetic diversity when it is not evidenced through the phenotype (Utter 1981; Tallman and Healey 1991; Freeman-Gallant 1996). Genetic information in concert with phenotypic, life history, and distribution information is the best way to identify appropriate units for conservation (Utter 1981). Integrity of groups having discrete spatial or temporal characteristics and genetic differences are routinely considered to constitute distinct populations. However, lack of either genetic or morphological distinctness alone should not be grounds for considering the taxon a homogenous unit (Utter 1981).

In the United States, species, subspecies, and significant populations threatened with extinction are protected under the Endangered Species Act (ESA). The ESA uses "evolutionarily significant unit" (ESU) to define populations qualifying for protection if their status is sufficiently threatened. An ESU is "a population (or group of populations) that 1) is substantially reproductively isolated from other conspecific units, and 2) represents an important component in the evolutionary legacy of the species" (Waples 1995). As discussed above, the

distribution of phenotypic diversity in a (sub)species provides critical information complementary to genetic diversity and life history information regarding the evolutionary direction and diversifying mechanisms within a taxon. Phenotypic variation gives biological meaning to genetic differentiation and adds evolutionary significance to short-term life history and animal movement information.

HABITAT MANAGEMENT AND RESERVE DESIGN

Diverse habitat across spatial scales is essential for the conservation of biodiversity (Franklin 1993). A reserve system and management of the medium surrounding reserves will be required to sustain species integrity. When habitat is not available, ecological processes can not continue (Meffe and Carroll 1994). Local adaptation is dependent on habitat heterogeneity, creating differential selection pressures between sites. Without maintenance of that heterogeneity, phenotypic and genetic diversity will be eroded. Genetic diversity preserved in isolation is insufficient for conserving species if suitable ecosystems and dynamic processes are not maintained (Meffe and Carroll 1994). Salmonid genotypes and phenotypes vary on multiple spatial scales and across habitats. Conservation of particular phenotypes will require conservation of the local population, in its habitat (Healey and Prince 1995).

Habitat reserves are an essential element in any comprehensive program to conserve biological diversity. Conserving biodiversity requires the maintenance of habitat across a wide array of spatial scales, and must include landscape and ecosystem approaches (Franklin 1993). Reserve designs for stream fishes should consider community-level biotic and abiotic interactions, relationships between habitat diversity and species diversity, the importance of disturbance in maintaining species diversity, minimum population sizes necessary to respond to the stochastic, demographic, and genetic effects of isolation, the value of peripheral populations that may be genetically or phenotypically distinct, and the necessity for redundancy to guard against catastrophic extinctions (Moyle and Sato 1991; Lesica and Allendorf 1995). Understanding of the historical nature of streams and stream habitat is critical to the restoration of conditions to which salmonids have adapted, and to the full expression of salmonid life history diversity (Lichatowich et al. 1995). In addition to reserve establishment, life history habitat relationships must be reestablished through restoration of watershed processes that produce high quality habitat (Lichatowich et al. 1995). Reserves must be of sufficient number and size and of appropriate distribution over the landscape in terms of geography and ecosystem type

(Franklin 1993). Detailed knowledge of species' requirements is required to design an appropriate reserve or reserve network (Wright 1990). Greater understanding is needed regarding the relationships between landscape scale for survival of metapopulations and scale of individual movements (Wright 1990). Reserve design should strive to maintain life history and genetic population structure, maintaining natural gene flow rates, effective population sizes, and extinction and recolonization probabilities (Meffe 1986; Porter 1999). Reserve design must also consider matrix conditions surrounding reserves, since refugees into reserves from nearby degraded habitat may disrupt natural genetic population structuring (Porter 1999). Similarly, complete reserve isolation by situation as an island surrounded by lost habitat may result in reduced gene flow, altered genetic structuring, and increased risk of extinction.

Conservation of species diversity in stream salmonid communities will require not only protection of streams but of entire watersheds. Reserves or lands set aside for aquatic species will likely not be able to be large enough to be the primary solution to loss of these communities (Angermeier and Winston 1999). Conservation of species population dynamics and landscape-scale processes are goals that must be met if stream salmonid communities are to be conserved (Reeves et al. 1995; Schlosser and Angermeier 1995).

REINTRODUCTION EFFORTS

Understanding the processes generating phenotypic diversity, the factors controlling its distribution, the scales at which it is distributed across the landscape, and its relationship to genetic diversity will provide essential guidance to reintroduction efforts for extirpated taxa. The importance of genetic and phenotypic structuring and links with environmental templates to success of reintroduction efforts is increasingly being recognized (Young 1999). He suggests that artificial reintroduction may be an important step in the restoration of Pacific salmon by hastening the natural processes of straying and colonization, rescuing metapopulation situations that may be on trajectories of extinction due to past habitat degradation and overharvest but which are now ripe for recovery and population reestablishment. He does, however, emphasize the importance of local adaptation and genetic structure in choosing source stocks, as well as the limited availability of empirical data on reintroduction (e.g. numbers of source spawners, source populations, releases, critical adaptive traits/taxon). Understanding the relative roles of environmental and genetic control over phenotype, and ultimately fitness, will contribute to more successful reintroductions into extirpated ranges for a species (Taylor 1991). Such information

will direct conservationists and managers with regard to the importance of genetic history of the introduced stock, the environmental conditions of those stocks, and the identity of critical phenotypic traits for the introduced stock (Echelle 1991; Taylor 1991).

CONSERVATION OF WESTSLOPE CUTTHROAT TROUT

Although westslope cutthroat trout historically were and currently are one of the most widespread of the inland trout, the subspecies is in decline through much of its range (Lee et al. 1997). Identified sources of decline include habitat degradation (Rieman and Apperson 1989), exotic species, and overharvest (Liknes and Graham 1988). Habitat fragmentation has also been cited as a cause of decline in westslope cutthroat trout communities (Liknes 1984; Rieman and Apperson 1989; Lee et al. 1997). Westslope cutthroat trout are currently extensively introgressed with rainbow and Yellowstone cutthroat trout throughout their range, pure westslope cutthroat trout being restricted to small isolated populations in headwater streams (Reinitz 1977). Strong populations of westslope cutthroat trout are estimated to persist in 11 to 22% of its historic range in Idaho (Rieman and Apperson 1989; Lee et al. 1997); Montana populations are in worse condition than those in Idaho (Liknes and Graham 1988; Shepard et al. 1997).

Westslope cutthroat trout distribution-habitat relationships are reviewed by Rieman and Apperson (1989), McIntyre and Rieman (1995), Lee et al. (1997) and McIntyre and Rieman (1995). Westslope cutthroat trout are generally associated with high quality habitat, cool temperatures, and limited sediment loads (Liknes 1984). Although they are often widely distributed within a basin in a variety of habitats, they tend to prefer smaller streams or backwaters and side channels of larger streams (Shepard et al. 1984). They are often found in moderate to high gradients (MacPhee 1966; Averett and MacPhee 1971; Shepard et al. 1984). Habitat use changes ontogenetically, with smaller individuals preferring shallow, slow water along stream margins and larger fish preferring deeper, faster water in main channel pools. Bozek and Rahel (1991) found that young cutthroat trout consistently preferred slow water and depths greater than 3cm, and were also associated with spawning gravel and avoided deeper water. Cutthroat trout tend to be closely associated with pools (Herger et al. 1996; Dunnigan 1997). Heggenes et al. (1991) found a composite habitat variable consisting of overhead cover and depth to best explain adult cutthroat distribution, with dominant fish occupying deeper pools. In southeast Utah, Colorado River cutthroat trout were more abundant and larger in habitats

associated with wilderness areas, characterized by more and deeper pools, more cover, and less fine substrates (Kershner et al. 1997). Lider (1985) concluded that cover diversity produced greater numbers of trout and a wider distribution of size classes. Habitat variables including cover, depth, percent pool, substrate size, and bank stability were associated with westslope cutthroat trout distribution in a Montana basin (Ireland 1993). Westslope cutthroat trout habitat use appears to differ when sympatric with competitor species such as coho salmon (Glova 1987; Bisson et al. 1988) and brook trout (Griffith 1972), with cutthroat trout occupying more marginal habitats in sympatry than in allopatry. Several variables at different scales, including habitat variables mentioned above, and geomorphic variables such as stream order and elevation were significant in explaining westslope cutthroat trout distribution in a Montana basin; location of spawning areas and wintering refuges were also likely to have affected fish distribution (Ireland 1993). In order to maintain the evolutionary potential of this species, diverse habitats across its range, and natural rates of gene flow between populations and larger spatial units, will be required.

Morphology of cutthroat trout has been shown to be variable. In forms showing no electrophoretically distinguishable genetic differences (Loudenslager and Gall 1980), Behnke (1988) found significant differences in pigment pattern and life history traits. Carl and Stelfox (1989) studied meristics, morphometry, and genetics of cutthroat trout from adjacent lakes in Alberta and found considerable variation in morphometry in the populations studied. However, no apparent effort was made to control for allometric differences. Meristic counts varied little, other than pyloric caeca and scale counts along and above the lateral line, which varied considerably. Little genetic variation was detected. Leary et al. (1996) studied the use of presence/absence of basibranchial teeth to separate rainbow trout, cutthroat trout, and hybrids of these taxa, and concluded through genetic confirmation that westslope cutthroat trout are naturally variable for this trait. Westslope cutthroat trout from a hatchery stock characterized by low heterozygosity had reduced developmental stability, including high frequencies of morphological deformities and bilateral asymmetry of meristic counts (Leary et al. 1985).

Multiple life history types have been documented for westslope cutthroat trout, and include resident, fluvial, and adfluvial types (Bjornn and Mallet 1964; Behnke 1992; Brown and Mackey 1995; Northcote 1997). However, much remains to be studied regarding genetic relationships and mechanisms encouraging development of these life history types. Variation in life history parameters including age and size at maturity, sex ratio, fecundity, and longevity

have been documented in westslope cutthroat trout (Downs and White 1997). They also found variability in age at maturity of westslope cutthroat trout in a Montana drainage; some females matured at age 3 and most by age 5; some males were mature at age 2 and all were mature at age 4. Gresswell et al. (1994) found Yellowstone cutthroat trout age at maturity to change over several decades and in conjunction with changes in harvest regulations in Yellowstone Lake. Westslope cutthroat also vary with respect to distribution of juvenile abundance and redds (Ireland 1993). Harvey (1998) found that coastal cutthroat trout exhibited considerable movement rates, and that smaller order streams tended to contribute considerable numbers of immigrants to larger downstream systems. Migratory and resident forms of westslope cutthroat trout may be at least partially reproductively isolated; Johnson (1963) found that migratory fish tended to spawn in lower reaches of the same streams used by resident fish. Westslope cutthroat trout of different life history types may express genetic differences as well as differences in life history traits. Growth conditions differ as well as other habitat conditions, suggesting differences in life history traits such as age at maturity and population size structure. The role of migratory life history types may vary across streams with different productivity and therefore growth conditions; low productivity streams may contain or produce more migratory individuals that leave natal streams early in life and return to only to spawn. Juvenile size structure may affect juvenile timing of downstream migration, since smaller individuals have poorer migration survival (Nicieza et al. 1994). Abundance and distribution of juvenile westslope cutthroat trout has been associated with spawning-sized gravels (Liknes 1984; Magee et al. 1996).

Salmonids in general are well documented for their frequent, complex, and diverse movement behaviors, including a variety of ontogenetic and seasonal niche shifts (Thorpe 1994). Although it has been thought that resident fishes in headwater streams move little, under certain conditions westslope cutthroat trout may move often and over relatively long distances (Bjornn and Liknes 1986; Fausch and Young 1995). Reported migrations of westslope cutthroat trout in the Flathead basin, Montana, include spawning and smolt migrations from tributary streams to winter refuges, juvenile movement downstream into larger systems, and movements into lakes and larger rivers in the case of adfluvial and fluvial stocks, respectively (Lukens 1978; Liknes 1984; Liknes and Graham 1988). Athearn (1973) found significant differences in migratory behavior of westslope cutthroat trout fry from different lakes that were apparently controlled genetically rather than being responses to factors such as food availability,

temperature, or water flow. Heggenes et al. (1991) found that most individuals of headwater populations of coastal cutthroat trout tended to remain static, with 32.4% of marked fish recaptured within 1m of their original capture site. Only 17.9% of marked fish moved more than 50m. Fish occupying pools moved less than fish occupying shallow habitats. The majority of each population was static, residing within a home range of less than $22m^2$. In a study of westslope cutthroat trout in a Montana basin, Ireland (1993) found 65% of tagged fish did not leave their habitat unit. Most fish that moved traveled distances of 0.5 to 1.0 km; 20% moved more than 2km. Movement of fish in downstream areas was more frequent and of longer distances than from headwater areas. Harvey (1998) found resident coastal cutthroat trout movement to be highly variable but high rates of movement, including long distance movement, were found from both simple and complex habitat types.

Quantity and distribution of genetic diversity within species is highly variable in salmonids, ranging from 65 (brown trout) to 95% (sockeye salmon) of genetic diversity contained within populations (Ryman 1983). Westslope cutthroat trout is more similar to brown trout in having a considerable portion of species genetic diversity distributed between populations and between drainages (Allendorf and Leary 1988), suggesting lower straying rates relative to other salmonids. They found genetic variation in a Montana drainage of westslope cutthroat trout to be distributed between drainages (16.7%), within drainages (15.7%), and within streams (67.6%). However, westslope cutthroat trout in the Coeur d' Alene River drainage of Idaho appears to be anomalous in that very little genetic differentiation has been detected between populations (P. Spruell, personal communication). Salmonid tendency to home to natal streams encourages genetic variation at local spatial scales (Riddell et al. 1981). Compared to other fish species, cutthroat trout populations appear to have relatively high diversity within and between drainages; most species surveyed contained 70-98% of diversity within populations. These authors found a considerable portion of alleles to be relatively rare, found in only one or two populations, and that they were relatively common within those populations. Since they may be at least partially reproductively isolated and reside for part of their lives in different habitat conditions, one might expect genetic differentiation between streams. Conservation of genetic diversity in this subspecies will therefore require protection of many populations within its range (Leary et al. 1988). This information supports the contention that westslope cutthroat trout consist of at least partially isolated populations with restricted gene flow between drainages and/or localized selection pressures.

Conservation of this subspecies will require maintenance of population structure, including natural rates of movement and gene flow between populations at multiple scales. The anomalous genetic structure of the Coeur d' Alene system should be further investigated. Establishment of protected areas should include pure stocks, diverse habitats, natural rates of gene flow, and particularly strong populations. However, management for the restoration of degraded systems should also be implemented and further degradation should be avoided. The role and spatial and temporal scales of natural disturbance in controlling population structure and dynamics of this subspecies should be investigated so that unavoidable anthropogenic disturbances can be designed to mimic natural patterns. Relationships between life history types should be investigated to determine levels of gene flow between them and mechanisms encouraging diversification. Relationships between westslope cutthroat trout and other species within their range should be investigated since conservation actions for this subspecies may not benefit, and could harm, sustainability of other species.

CONCLUSION

Most North American salmonid species and lower taxa are in decline, due to habitat degradation, overharvest, genetic degradation, and other causes. Considerable effort is currently being expended to reverse population declines and loss of diversity within and between stocks. Conservation theory is being widely applied to salmonids, with some success. However, much information remains to be gathered before conservation needs of salmonids can fully addressed.

Phenotypic variation provides the flexibility within a species to allow response to short term environmental variability, through plasticity, and evolutionary time-scale variability in environmental conditions, through local adaptation and natural selection. Phenotypic diversity is the variation in life history, behavior, and morphology of organisms due to genetic differences between individuals (genetic variation), the flexibility in an individual to allow it to adjust to changing and diverse conditions (plasticity or environmental variation), and combinations of and interactions between the two. Phenotypic variation is spatially distributed as a product of its genetic and environmental origins. The genetic diversity of a taxon is distributed in a spatial hierarchy as a function of gene flow, and environmental variation is distributed in a clumped and patchy manner at various scales. Phenotypic variation therefore is spatially distributed in

patterns that should be predicable if historic relationships of the taxon with its environment are understood. Unfortunately, this understanding has not yet been achieved with salmonids, especially stream-dwelling salmonids, although considerable empirical effort has been accomplished and is available for application to conservation efforts.

Salmonids have exceptional levels of intraspecific variation. Their habit of homing to natal streams, and occupation of diverse and geographically distant habitats that can be characterized by a diversity of disturbance regimes, creates a template for diversification as a product of restricted gene flow between populations and local adaptation. Phenotypic variation in morphology, behavior, and life history characteristics has been well-documented for many salmonid species, as a product of both genetic structure and environmental variables. However, taxa and life stages are differentially sensitive to their environment, and level of variation differs between taxa. Taylor (1991) and Winemiller and Rose (1992) provide valuable reviews of phenotypic variation in salmonids.

Conservation of salmonids must focus on three critical components of diversity within a taxon: genetic diversity and diversifying processes, population structure, and the environmental template. Only with full consideration of these issues, and their application to relevant conservation efforts, can the full complement of diversity with a taxon be conserved across immediate, mid-term, and evolutionary time scales. Reserve/refuge design, habitat management and restoration, maintenance of evolutionary potential and processes, articulation of conservation units within political and legal arenas, and conservation of multiple species and levels of biodiversity can not be accomplished without understanding the genotypic and phenotypic legacy of a taxon and the processes and conditions that generated it. The westslope cutthroat trout is a valuable, yet typical, example of the challenges inherent in conserving stream salmonids. Its spatial distribution across diverse habitats and the distribution of its genetic and potentially phenotypic variation at local spatial scales requires conservation of multiple populations, natural restricted gene flow rates, and at least a representative portion of its habitat.

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